

No. 3 — *Studies on Deep-sea Angler-fishes (CERATIOIDEA)*¹

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I. An historical survey of our present state of knowledge

In 1833 a strange and theretofore unknown fish was thrown up on the beach near Godthaab, Greenland, after a severe storm. It was remarkable for its bulky rounded body lacking ventral fins, black skin sparsely set with large spine-bearing plates, and especially for the "frontal tuft" arising from a longitudinal trough on the forehead and terminating in a bunch of filaments. Captain-lieutenant Carl Holböll procured this fish, unfortunately badly damaged by birds and decay, and sent it to Prof. Joh. C. Reinhardt at Copenhagen. The latter in 1837 described the specimen, which was fifty-eight centimeters in length, as adequately as possible under the circumstances and named it *Himantolophus groenlandicus*. Because of the lack of proper material for study, Reinhardt was not explicit in placing his type in any of the known groups of fishes, but his comparison of this new form with *Antennarius* and *Lophius*, especially with reference to the "Pandusk," or frontal tuft, of *Himantolophus*, which he thought to be the same structure as, but more highly developed than the first dorsal ray on the head of *Lophius*, indicated that he believed his species to be related to those fish which comprise the Order *Pediculati* (Regan 1912). *Himantolophus groenlandicus* was the first deep-sea angler-fish to be discovered.

Before 1845 the same Captain Holböll who had collected this *Himantolophus* had obtained from the deep-sea off Greenland two more new "barbugede Tudsefiske" (called bare-bellied by the Danes because ventral fins are lacking in all the known ceratioid pediculates). One of these two was described in 1844 by Prof. H. Krøyer as *Ceratias holbölli*, while the other remained unnoticed, at least in the literature, until Prof. Chr. Lütken rescued it from dusty oblivion and described it as *Oncirodes eschrichtii* in 1871. Today these first specimens are considered members of three distinct families of the Suborder *Ceratioidea*.

After these first ceratioids from high latitudes were discovered, occasionally others were taken, usually only a single specimen, sometimes taken floating helplessly on the surface, as was *Melanoectus*

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johnsonii Günther with another fish two or three times as long as itself coiled up in its stomach (Regan 1913). It was not, however, until the great oceanographic expeditions of the last fifty years or so that these peculiar fish were taken in any numbers. By far the most notable contributions to our knowledge of the *Ceratioidea* have come from the Danish oceanographic expeditions on the "Dana" under the leadership of Johannes Schmidt. The 1920-22 Expedition took more than three times as many specimens as had probably been caught altogether up to that time and more than doubled the number of known species (Regan 1925a, 1926), and the 1929-30 Voyage-around-the-world again more than doubled the described ceratioids (Regan and Trewavas 1932) bringing the total, including those more recently described by Parr (1934), Schultz (1934), Fraser-Brunner (1935), and Belloc (1938, p. 303-6) to one hundred and sixty-four species.¹

Since about eight hundred and sixty specimens are recorded in the literature, this would average five specimens per species. The distribution of specimens has not, of course, been so fortunate, for two of the eleven families, twenty of the forty-one genera, and one hundred (or 61%) of the species are known from single specimens only. A mere handful of species are known from a sufficient number of specimens to allow any accurate ideas to be formed on their vertical and geographical distribution, changes in various parts and proportions in different stages of development, variability within the species, and many other such fundamental problems. There thus remains a tremendous amount of further collecting and comparative study of many more specimens before any adequate generalizations may be made concerning the biological relationships of these weird deep-sea fishes.

It was believed from an early date that the ceratioids were deep-sea fish, "degenerate" relatives of *Lophius piscatorius* L., living on the bottom with habits generally similar to those of this latter form. A species of *Lophius* common in the Mediterranean was well known to the ancients by such apt names as *βάτραχος ἀλιεύς*, *Rana marina*, *Rana piscatrix*, and the like. From the time of Aristotle vivid accounts were written of how this sly fish would use its frontal filament, or illicium, for attracting prey. The following passage (p. 67) from Oppian's "Halieutica," which was probably written in the reign of Marcus Aurelius (Emperor 161-180 A.D.), is an interesting example.

Most of the Renaissance ichthyologists, Rondelet, Belon, Salvianus and others, have passages describing similar behavior in *Lophius*. Ulyssi Aldrovandi in his "De Piscibus" (1612, p. 454-70) gives a non-

¹ *Oncirodes bulbosus* Chapman (Proc. U. S. Nat. Mus., Vol. 86, p. 538, 1939) brings the total up to one hundred and sixty-five.

gustatory, since they were well supplied with nerve fibers, on the bait or esca of the frontal filament of *Gigantactis*. None the less, there would appear to be a considerable amount of truth in the old stories about *Rana piscatrix* since recent observations of this fish in its natural habitat such as those cited by Bigelow and Welsh (1925, p. 528) and those of Chadwick (1929) and Wilson (1937) on aquarium specimens indicate that a *Lophius* lying concealed on the bottom indeed often does lure other fish towards its waiting mouth by waving back and forth over its head the first dorsal spine with its terminal tag-like expansion.

This is undoubtedly true also of *Antennarius*, the frog-fish, another well-known shore water pediculate. Louis L. Mowbray, Esq., Director of the Bermuda Aquarium, has many times over a course of years observed the angling activities of aquarium specimens of this genus (personal communication 1938). When other small fish were placed in its tank, the *Antennarius* would slowly maneuver into a position near these other fish and begin to "angle." This consisted of moving about the rod-like first spine of the dorsal fin with its fleshy terminal expansion in a characteristic manner which was different in some cases for different kinds of prey. For example, when one kind of fish was in the tank with the *Antennarius*, it might slowly draw the first dorsal ray through the water in such a way that the "bait" moved back and forth in a sweeping arc, but when another kind of fish was present, it might vibrate the first dorsal ray and thus merely shake the "bait."¹ Any fish which ventured near the *Antennarius* to investigate the moving "bait" was drawn very quickly into the enormous mouth cavity of the frogfish by a sudden gulp.

Histrio, the closely related Sargassum fish, which has taken up the specialized habitat of floating Sargassum weed, has also been observed many times under similar conditions, but interestingly enough, this fish has never been seen to use its first dorsal ray as a lure for prey but appears rather to depend entirely in obtaining its food on stealth and its inconspicuous appearance, which resembles remarkably that of the Sargassum to which it clings.

Samuel Garman (1899) in his description of the *Pediculati* from the "Albatross" collection of deep-sea fishes introduced two useful terms in referring to the frontal filaments of the fishes in this order. The whole first dorsal ray with its terminal elaboration he called the illicium. This was a Latin word meaning lure or inducement; it was

¹ Wilson (1937, p. 488) similarly describes two comparable types of angling movements in *Lophius*.

not, however, at all frequently used by known Latin authors, and I have not been able to find it once used or referred to in any biological context earlier than Garman's, although a number of Latin authors used the related verb forms such as that seen in the quotation from Rondelet given below. According to Dr. Thomas Barbour (personal communication 1938), who was at the time a student in Garman's laboratory, Garman himself believed that he was coining a new biological term in *illicium*. Regan (1912), recognizing its usefulness, used the word again, and since that time it has been generally employed.

Garman called the terminal elaboration of the first dorsal ray the *esca*; this was a Latin word meaning bait, which had frequently been employed since classical times in reference to the use to which *Lophius* allegedly put its frontal filament. Cicero (ca. 45 B.C.) used *esca* in a description of the fishing frog's feeding habits in his "De Natura Deorum" (Lib. II, No. 125) ". . . ad quas quasi ad escam pisces quum accesserint . . .", and nearly all of the Renaissance natural history writers whom Needham has called the macro-iconographers of the sixteenth century, employed the same word similarly. Rondelet, for example, in his "De Piscibus Marinis" (1554, Lib. XII, Cap. XX) used it in the following passage concerning *Lophius*: ". . . ante (oculos) propendent appendices duae . . . quibus veluti esca pisces mira solertia allicit et capit quod non solum gravissimo Aristotelis testimonio, sed etiam piscatorum multorum experientia comprobatum est." It would seem obvious that Garman, who was a fine scholar of the old literature, had the term in question from such sources. *Esca* has not been used in recent ichthyological writings except by Garman, but I feel that the word would be a useful and convenient one to reintroduce.

Thus when Reinhardt (1837) described the *illicium* of *Himantolophus* as being the same as, but more highly developed than the fishing filaments of *Antennarius* and *Lophius*, he certainly implied its use as a lure. Lütken (1871), however, seems to have been the first to state this directly, and he even suggested that the shape of the *esca* and its tentacles in *Oneirodes* might resemble the head of a nereid worm. The fact that some parts of the *esca* in at least certain of the ceratioids were luminous was first mentioned by Willemoes-Suhm (1876) in his letters from the "Challenger." This luminescence was thought to make the *esca* effective in the "eternally dark abysses" of the oceans, where it could not otherwise be seen.

Brauer (1908) in the anatomical section of his classic work on the "Valdivia" deep-sea fish made histological studies of the *illicium* and

its terminal light organ in *Gigantactis* and *Dolopichthys* (which latter Brauer identified as *Oneirodes*). The light organ was described as a spherical, hollow, glandular structure located within the swelling of the esca and surrounded by a layer of reflecting cells and a heavy black pigment capsule. The lumen of the gland was filled by small granular bodies which Brauer considered to be secretory granules produced by the gland cells, some of which could be seen in his preparations breaking down and apparently releasing from their cytoplasm similar structures into the cavity of the organ. This lumen opened into a second, more distal cavity which in turn communicated with the exterior by a canal opening on the mid-dorsal line of the swelling of the esca. Because of its general structure and especially because of the presence of the external opening, Brauer believed this organ to be a "Spitzdrüse," that is a gland whose secretions were forcibly ejected. Never the less, he could not find any muscles in the esca which would permit such an active emptying of the gland's lumen. Neither was he able to find any nerve supplying the light organ although, as mentioned above, branches of an illicial nerve were distributed to the apparently sensory papillae of the esca. A fairly good blood supply, on the other hand, was found running to the luminous gland.

Similar terminal glandular organs may be present on other median fin rays of ceratioids such as those described by Brauer in the caruncles of the dorsal fin in *Cryptosparas*. As was noted by Regan (1926, p. 11) large specimens of this same genus may even have such structures present on the rays of the caudal fin. Luminescence has been observed by several workers to occur in the esca light organ, and Beebe (1934, p. 191-2) observed light coming from swellings on the tips of the first three dorsal rays in a ceratioid seen by him from the bathysphere; whether all such swellings on ceratioid fins are luminous or not is not known.

Dahlgren (1928) without more than merely stating that such was the case, described from histological examination the granules filling the cavity of the esca light organ of a specimen of *Ceratias* as luminous bacteria. He presumed that these organisms were living symbiotically within the esca, supplying light for the fish's bait in return for nutriment provided by a sort of culture medium maintained within the luminous gland by the activity of the secretory cells. A similar type of symbiosis had previously been described for the light organs of three or four other fishes, in some of which the results were quite convincing since careful bacteriological methods had been employed. (Dahlgren gave several references; see also Yasaki and Haneda 1936).

This same sort of interesting relationship has been found to occur in a number of luminous cephalopods. Bacteriological investigations of the light organs of a considerable number of different kinds of these animals (Kishitani 1932, Herfurth 1936) have shown that only in the case of luminous organs which open to the exterior by a canal or pore were symbiotic luminous bacteria present in large numbers; those light organs which were closed to the sea water did not contain the symbionts. The light organs of all the fish which were believed to cultivate luminous bacteria in their lumina were also open to the exterior. Dahlgren's conclusions concerning the bacterial origin of the light in *Ceratias* were thus in general agreement with such studies. However, in the case of another fish, the macrurid, *Malacocephalus laevis*, in which the light organ was open to the outside the luminescence was apparently not a bacterial luminescence since microscopic study demonstrated that the granules present in the material filling the lumen of the gland were not bacteria (Hickling 1925). Furthermore, the test for luciferin and luciferase,¹ "substances" known to be involved in the luminescent reaction of a number of different organisms was positive. These materials have never been convincingly detected in bacteria so that it would appear highly unlikely that they were being extracted from symbiotic luminous bacteria in this case. It is clear then that at least two methods of producing light are employed by fishes, and it is possible that combinations of the two may be found in the same animal, but only after many more, careful investigations of the various types of luminous fishes and their light organs will it be possible to draw any satisfactory general conclusions concerning these matters.

Several references in the earlier literature to cases where living ceratioids were examined in the dark, state that the light produced by the esca light organ was apparently under "voluntary" control; this meant at least that the luminescence was not continuous. In 1936 I had the opportunity to observe a living *Dolopichthys* which was taken by the research ship "Atlantis" in the Sargasso Sea. Still feebly moving this specimen was quickly removed from the net and placed in cold water. In the ship's dark-room, I was able to observe the luminescence of the esca light organ during the ten minutes or so that the fish remained alive. This remained dark until the fish was quite actively stimulated mechanically. When it did luminesce, the light was confined within the esca, which was transparent and more or less free from pigment

¹ See E. N. Harvey. 1935. Luciferase, the enzyme concerned in luminescence of living organisms. *Ergeb. Enzymforsch.* Bd. IV, S. 365-79.

distally, and no trace of luminous secretion was observed to be extruded from the external pore of the organ. The light was bluish green in color like that of the majority of luminous organisms and lasted for five or six seconds beginning dimly and rising to a peak in a second or so, maintaining the maximum intensity for several seconds, and then slowly fading out.

If the luminescence of ceratioids is a bacterial luminescence, the question of the control of the light is a very interesting one, for luminous bacteria under normal conditions luminesce continuously, unlike all animals which produce their own light. A simple method of control of the light of these symbiotic bacteria would be through the amount of oxygen available to the bacteria, which luminesce only under aerobic conditions. It is bacteriologically conceivable that anaerobic conditions could be easily developed within the lumen of the light organ which would, when they became completely anaerobic, extinguish the light entirely. Sufficient oxygen for luminescence (the amount necessary is extremely small as was shown, for example, by the experiment of Beijerinck (1902) in which sufficient oxygen for momentary luminescence of the previously dark bacteria was obtained in a suspension of clover leaves illuminated by the light of a single match) could easily be supplied by a blood system such a Brauer (1908) described in the ceratioids he studied. The present very imperfect state of our knowledge of the physiology of bioluminescence makes it unwise to do more than outline a few of the more salient points in this connection. Certainly the problem of the control of luminescence in animals is one of the least understood, yet biologically one of the most interesting of the many aspects of bioluminescence.

The nineteenth century students of ceratioids believed that these fish were benthonic, like *Lophius*. Fillhol (1885, p. 81) even has an imaginative picture of *Melanocetus johnsonii* Günther in which several specimens are shown buried up to their eyes in the mud with their illicia waving over their heads. The fact that the mouth in this species opens upwards at a sharp angle made it a bit difficult to make these fish look plausible buried tail-downward in the ooze of the ocean bottom. Garman (1899) in his discussion of the genotype of *Dolopichthys* remarked on the improbability of such fish being active swimmers and stated his belief that their peculiar body form, fin reduction, and smooth skin were adaptations for life in the soft muds of the sea floor. It was Brauer (1906) who first showed that the ceratioids were bathypelagic rather than benthonic forms. He based his demonstration mainly on the analysis of vertical closing net hauls made by

the "Valdivia" and which showed at what depths in the water the specimens were fished; he furthermore pointed out that several ceratioids which had been taken previously had been found with scopeline and other non-benthonic fish in their stomachs. It is generally believed today that, with the exception of the young, which have often been taken in shallower water, the deep-sea angler-fishes live bathypelagically largely at depths ranging from 500-5,000 meters (Regan and Trewavas 1932, p. 12; Beebe 1937, p. 207).

The occurrence of dwarf males living attached to the relatively gigantic females which has been described in a number of deep-sea angler-fish is such a striking and bizarre phenomenon that it has become a part of everyday scientific knowledge. Nevertheless, no thoroughly satisfactory analysis of the few available facts concerning this interesting sexual relationship of the ceratioids has as yet been published. Regan and Trewavas (1932) give a good descriptive section on sexual dimorphism, however.

Saemundsson (1922) was the first to discover the attached males. He noticed two small fish grown fast to the belly of a large female *Ceratias holbölli*; he did not recognize them as dwarf males but thought that they might possibly be young of the same species since they showed certain well marked similarities to the larger fish. Three years later Regan (1925b) from a dissection of another specimen of *C. holbölli* to which a small fish was attached showed that this latter was a male with a fairly well developed testis and that the larger fish was a female.

Up to the present time fourteen specimens of these dwarf males have been discovered attached to twelve (out of the approximately five hundred and fifty known) female ceratioids. Most of these females had only one male grown onto them, but Saemundsson's specimen as mentioned above, had two, and one female of *Edriolychnus schmidti* (Regan and Trewavas 1932, plate IX, fig 2) had three of them. The males have been found attached head-on to the females by outgrowths from either the lower jaws or from both the upper and lower jaws to a papilla raised up on the surface of the body of the females. The place of attachment was apparently random since males have been found fastened to the belly, head, and even the preopercular spine of the females.

The female angler-fish so far found with attached males belong to four distinct families of the Sub-order *Ceratioidea*. Regan (1925, p. 397) at first believed that attached males were characteristic of the whole sub-order; this point of view was also favored by Parr. The latter worker, however, (1930) after a study of the anatomy of the

then rather anomalous family of ceratioids, the *Aceratiidae*, was led to conclude that these small fish, lacking an illicium externally at least (except for *Anomalophryne* Beebe, 1929) and generally possessing pincer-like rostral denticles, large nostrils and olfactory organs, were free-living stages of male ceratioids theretofore recognized only in the attached forms. A careful study of the viscera of one of these free-living non-illiciate fishes, *Rhynchoceratias longipiinnis*, was made by Parr (1930). This specimen was indeed a male and had a testis apparently as large relatively as any found in the attached males which have been investigated in this respect. Determination of the sex of as many of the aceratiids as possible has led to the discovery that they were all males; furthermore, similar study has shown all the illiciate "typical" ceratioids to be females. From anatomical evidence it has been possible in most cases to assign the free-living males to families previously known only from females. Free-living males then have been found to occur in five of the eleven families of the *Ceratioidea*.

Parr (1930, 1932) suggested that the free-swimming males were doubtless merely at an earlier stage in their life history than were the attached males and would consequently become attached at some later time. On the other hand, Regan and Trewavas (1932, p. 20) thought it probable in view of Parr's discovery of the free-living males, that attached males occur only in the four families in which they had been found up to that time and that all the other families of ceratioids had free-living males. This point of view was not sustained by any direct evidence presented but seemed rather to rest on Regan's (1925b, p. 396) assumption which he had maintained from the beginning that the attached males became fastened to the females at an early stage, probably shortly after the larval stage, certainly before the gonads have matured.

Evidence for a long period of attachment at least was found (Regan and Trewavas 1932, p. 42) in the skull of an attached male *Ceratias holbölli* in which certain osteological peculiarities were believed to have resulted from the male's having been much smaller at the time of attachment. However, if Regan's original assumption corresponds to the facts then no free-living males with as well developed testes as *Rhynchoceratias* could be found in a family which had parasitic males. Yet free-living males have been found in the *Linophryniidae*. Thus the situation becomes rather confusing in the paragraphs concerning the male linophrynids (Regan and Trewavas 1932, p. 15ff) since both free-living and attached males are described in this family. The free-swimming males of the type of *Aceratias* were shown to be very similar

to the attached males of the Genus *Borophryne*. In spite of the fact that the free-living male *Linophrynidæ* listed by Regan and Trewavas (1932) average over twenty-five percent longer in standard length than the attached males discussed, these authors felt obliged to maintain without qualification the assumption of an early time of attachment and the double hypothesis that free-living males occur in certain families of ceratioids and attached ones occur only in the remaining families. These views would seem to be rather troublesome to maintain especially since Parr's (1934, p. 56ff) discovery of a free swimming male, *Borophryne masculina*, belonging to a genus in which two females with attached males are already known. In this case, too, the free-living male is somewhat larger than the attached ones of the same genus.

It would thus seem clear that the simplest reasonable explanation of the facts would be that free-living and attached males might well be found to occur in all of the deep-sea angler-fish which have developed a marked sexual dimorphism. Furthermore, as Parr has pointed out (1930, p. 134), the males do not generally become attached at an early stage of their development since, for example, amongst the *Linophrynidæ* mentioned above there are one hundred and thirty free-living males recorded in the literature and only eight attached males. The time of attachment and consequently the period during which this union of male and female lasts would appear from the evidence reviewed to vary with the individual circumstances.

It has been generally assumed that the development of males which were first free-swimming fairly active fishes and then sessile on the females was an adaptation to the fact that the female ceratioids were solitary sluggish animals whose chances of mating in the dark abysses of the oceans would be rather negligible if the males of the group were of similar habit. This adaptational point of view would go on to suggest that if a male and a female of the same species were so fortunate as to find one another, some means of their continued association until their reproductive functions had been discharged would be of great advantage. Thus it may be that certain of the individual males find and attach on to their mates soon after the post-larval period, whereas others swim about seeking mates until they have become mature, and doubtless still other males never do find a female of their species. Also it may be in the more primitive families of the sub-order, in which no attached males have yet been found, that instead of actually growing fast to the females, as was the case of the attached males already known, the males merely nip on to the females for a relatively short

period. The fact that only two percent of all the known female ceratioids and only seven percent of the females of just the families in which attached males have already been described have males attached to them may be indicative of a relatively brief period of union between the two sexes. On the other hand, it may rather indicate, in conjunction with the very small size of the great majority of the angler-fish which have yet been captured, that only a relatively few mature fish have been taken so far.

Another point of interest concerning the male ceratioids is that although fifty-seven percent as many free-living male specimens as females have been found, there are only twenty percent as many species of males as there are female species. Thus there are not nearly enough species of males to pair them up with the females. If all the specimens which are assumed to be female are, it would seem likely then that either differences which were either individual or ontogenetic have been used in defining many of the female species, or else the ability to differentiate between males of different species has not been sufficiently developed to distinguish the rather obscure details which separate them.

The fact that both the *Melanocetidae* and the *Himantolophidae*, the most primitive families of the *Ceratioidea*, have two genera of males to one of females has been pointed out by Regan and Trewavas (1932, p. 21) to be in striking contrast with the rest of the sub-order. The fish in one of the male genera in both cases, *Centrocetus* and *Lipactis*, were more like females in shape than any other known free-living males; teeth in the jaws, which were generally absent in male ceratioids, were present, and the rostral denticles were not well developed. The more typically ceratioid appearance and the very small size of these peculiar males would suggest the possibility that they were merely juvenile specimens. A minute male of the Family *Dicraetiidae*, *Caranactis pumilus*, would presumably belong in the same category.

The physiological significance of the attachment of the males to the females in the deep-sea angler-fish is a point of great interest. Regan from his first paper on the subject has maintained that the attached males were nutritional parasites on the females. Sections cut through the region of attachment of the two fish were believed to demonstrate a complete blending of the vascular systems in that region indicating that they were continuous from one fish to the other (Regan 1926, p. 12). Furthermore, the mouth of the males, because of the nature of the attachment to the female, was no longer available for active feed-

ing, the stomach and gut were remarkably degenerate, and the union between the two was believed to last for a long time. All of these conditions would seem to indicate that the males must depend on some unusual source of nourishment. Further descriptions and figures of the region of fusion between the male and female, as it appeared in serial sections, were given by Regan and Trewavas (1932, p. 21); sinuses of the region were traced out as connecting the blood vessels of the pair through a capillary network on each side, thus proving the direct continuity of the blood streams that had been strongly suggested by previous studies. Parr (1930, 1932), however, expressed the opinion that the nutritional aspects of the continuity of the circulatory systems might not be as important as previously believed. He was led to this point of view, among other things, by the relatively enormous size of the liver in the specimen of free-living male whose anatomy he had investigated. Thus before the time of its attachment to the female, the male might store up a large quantity of food in its liver, which would be an efficient storage space; this food could then be used by the male during the period of his union with the female. Evidence in support of this suggestion may be obtained from a number of figures in Regan and Trewavas (1932, pp. 16, 17, 20, 22) of the visceral anatomy of male ceratioids. These figures show that the free-living males had relatively large livers whereas in the attached males which have been examined the livers were small. It is interesting to note in this connection that the attached male of *Ceratias holbölli* which Regan and Trewavas believed from osteological evidence to have been fastened to the female for a long period had apparently an extremely minute liver since this organ was neither shown in the figure of the anatomy of this fish nor mentioned in the text (Regan 1925b, fig. 4 and p. 392). Perhaps in cases where the attachment of the male lasts over a longer period than could be supplied with food stored in the liver, the nutritional possibilities of a confluence or even placenta-like arrangement of the blood streams may come to be realized.

A further structural arrangement pertinent to these matters has been known from the time of Saemundsson's (1922) discovery of the first attached male. Namely, the fact that in every case although the mouth of the attached fish becomes more or less occluded from the nature of the attachment, lateral openings into the mouth cavity are retained. These are believed to permit the circulation of a respiratory current. Regan (1926, p. 14) stated that since the attached males have a well developed heart and gills, they do not depend on the blood of the females for oxygen but only for nutritive materials. As Parr

(personal communication 1938) has pointed out, if arrangements for a respiratory current and normally developed respiratory and circulatory systems are maintained by the attached males, they could not be receiving sufficient oxygenated blood from the females for their own, probably meager, needs. Either then the male receives only venous blood from the female or else not much blood at all. Two facts would appear to cast some light on the probability of the former alternative: First, Regan (1926, p. 14) states that both arteries and veins run into the capillary network of the tissues connecting the males and the females. Second, if the males were carrying the added excretory burden of a considerable venous circulation from the females, unusually large kidneys might be expected in the attached males; these organs have not been found to be of greater size⁸, however, than those found in the free-living males. If these arguments carry any weight, then we are left with the alternative that there is not much blood interchange between the males and the females.

One idea that has been suggested by both Regan and Parr is the possibility that the continuity of the blood streams would permit an hormonal interchange between the male and the female which might affect the differentiation of the gonads, and synchronize their maturation and the discharge of their sexual products. However, from the general results of vertebrate endocrinology, especially as related to parabiosis, it would appear unlikely that the attachment of the males, provided they were sexually differentiated (and there is no mention in the literature of any attached "male" in which the gonad could not be easily identified as testis) and normal as to their endocrine functions, was of any particular significance (Hisaw, personal communication 1938). It must be admitted, never the less, that in animals which have become morphologically as highly specialized as the ceratioids it would be difficult to predict with any degree of assurance what special physiological functions they may have developed in the course of their evolution.

The foregoing account has attempted to outline and assay the facts which are known concerning the deep-sea angler-fish. In the analysis of even the most recent knowledge of these fish the discussion has been filled with probabilities, suggestions, ideas, possibilities, and the like, and nearly every problem approached was found to rest in a highly unsettled and hypothetical state. This at the present time is true of our biological knowledge of all bathypelagic organisms. The great difficulty and expense of obtaining material and the well nigh insuperable barriers to experimental work in this field have been the

principal deterrents to great advances in these directions. It is to be hoped, however, that in the future with the further coöperation of the great oceanographic institutions and their research vessels that many of these intriguing and significant problems may be satisfactorily solved and fitted into the general body of physical and biological knowledge which constitutes the science of oceanography.

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II. Three new species

In the course of examining hauls made from the research ship "Atlantis" during the summers of 1936 and 1937 a few small *Ceratioida* were found. Three of these are apparently new species belonging to 3 distinct families of this suborder: *Gigantactinidae*, *Linophrynidae*, and *Oncirodidae*.

GIGANTACTIS LONGICIRRA, spec. nov. (Figs. 1 and 2)

1 specimen: holotype, M. C. Z. No. 35,065.

Total length about 62 mm., standard length 39 mm. Illicium terminal on snout, length from articulation with basal bone to distal end of the bulb 15 mm. (39% of S. L.). Length of lower jaw 7 mm. (18% S. L.); eye diameter 0.8 mm. (2% S. L.).

Fin rays. D.8, A.6, C.8, P.18. Branchiostegal rays 6 (2+4); pectoral radials (pterygials) 5 (4+1).

Dentition. All teeth curved and depressable inward or backward. Lower jaw: 13-14 teeth on each side, of different sizes, ranged in 2 rows one within the other. Upper jaw: 8 in a single row on each premaxillary; maxillary toothless. Lower pharyngeals toothless; upper pharyngeals: 2nd and 3rd pharyngobranchials each have 3-4 large teeth. Palatines and vomer toothless.

The esca¹ (Fig. 2) consists of a somewhat pear-shaped swelling, rounded and blunt distally, and bearing at its proximal end 20 slender filaments which are 60-300% as long as the swelling itself. Each of these filaments terminates distally with a just perceptible bulbous expansion. Within the pear-shaped swelling is a heavily pigmented spherical core (the light organ) with a hemispherical prominence of about half its own diameter projecting from it postero-dorsally. The core is borne on the larger end of a conical expansion of the inner stalk which runs up the center of the illicial stem.

The nostrils are tubular; lateral line organs on projecting tags or flaps of pigmented skin are present on the head, body, and also the rays of the caudal fin. There are no channels or grooves connecting these organs with one another. The skin is closely set with small sub-circular plates each bearing a short sharp spine.

No pelvic bones were found in a dissection of one side of the specimen.

¹ For definition and origin of this term and "illicium" see preceding section, p. 68-9.

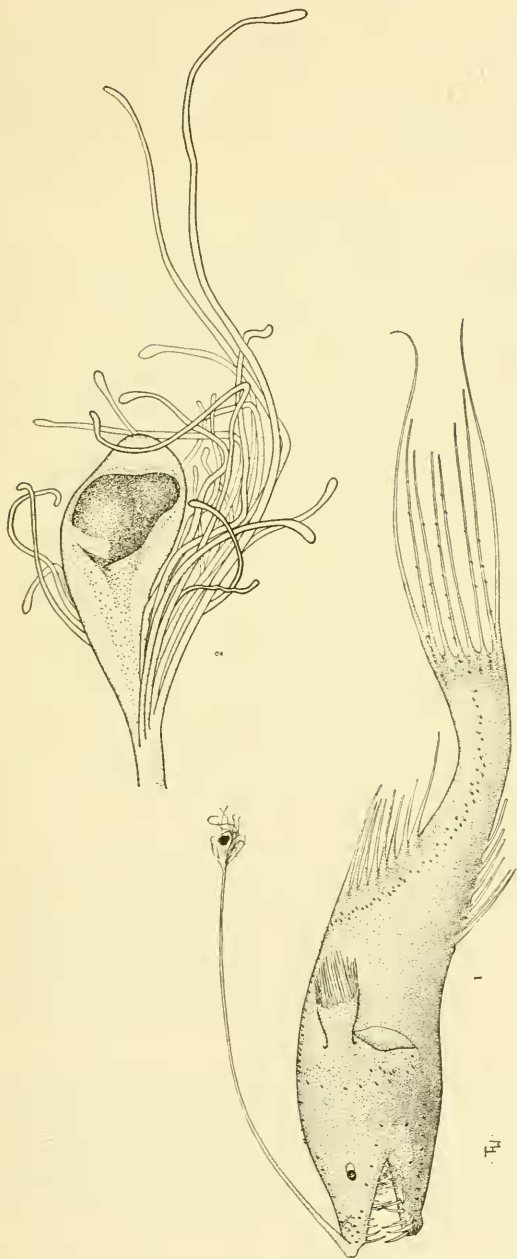


Fig. 1. *Gigantactis longicirra*, spec. nov. Standard length 39mm.

Fig. 2. Lateral view of esca of *Gigantactis longicirra*, spec. nov.

Color. Chocolate brown (after fixation in formalin, followed by alcohol.)

Type locality. "Atlantis" Station 2894, July 20th, 1937, continental slope about 300 miles east of Cape May, New Jersey (39°06'N., 70°16'W.), closing net at 1000 m., 4 A.M., depth to bottom 2860 m.

Discussion

Clearly the slender, elongate body of this ceratioid, the attenuate frontal region of its skull, and the long illicium located terminally on the snout demonstrate that it belongs to the *Gigantactinidae* Boulenger, 1904, and more specifically to the genus *Gigantactis* Brauer, 1902. Of the 8 individual specimens of the genus, which have been taken previously, 7 are types of as many different species (Brauer, 1902; Regan, 1925, 1926; Regan and Trewavas, 1932; and Fraser-Brunner, 1935) from all of which the present specimen is notably distinct. Four characters clearly set it apart from any other known form. These are:

1. The number of dorsal rays is greater by 2 than that given for any of the other *Gigantactinidae*; all other members of the present genus have 6 and *Rhynchactis leptoneura* 3 (Regan, 1925)¹.

2. In the pectoral appendage one more pectoral radial bone is present than has been described for any of the other *Pediculati*, which primitively have only 3 of these bones (Gregory and Conrad, 1936, p. 202). Regan and Trewavas (1932) have found 4 of these elongate basalia in both *G. sexfilis* and *Rhynchactis leptoneura* and suggested (p. 25) that the presence of 4 of them is a diagnostic feature for the *Gigantactinidae*.

3. The length of the illicium from its proximal end, where it articulates with the modified pterygiophore or "basal bone," to the distal end of the bulb of the esca is less than 40% (38%) of the standard length. In previously known species, including smaller as well as larger specimens, this measure was always 60% or more of the standard length, varying from 60% in *G. exodon* (where it might be a juvenile character since the type is only 25 mm. in standard length) to 400% in *G. macroneura*.

4. The esca is notably different from that described for any other ceratioid. Except for *exodon*, all other gigantactids have terminal filaments present on the esca whereas in the present fish there is no

¹ Only 5 dorsal rays are shown in the figure of *G. vanhoeffeni* although 6 is the number given in the description (Brauer, 1906).

trace of such. In *exodon*, however, the swelling of the esca tapers distally; this is definitely not the case with the new species. Yet in the only other species of *Gigantactis*, *orifer* and *flibulbosus*, in which the bulb does not taper distally there are two terminal filaments present in the esca and no proximal filaments at all. The proximal filaments of the new species' esca are more numerous and longer proportionately than any such filaments found in other specimens of *Gigantactis*.

A further point of interest in *G. longicirra* concerns the lateral line organs. In other members of the family (Regan and Trewavas, 1932, p. 24) these occur on "stalks" rather than on "tags" as found in *longicirra*. If this difference does not depend on confusion of terminology it may well be a fifth clear distinction of the present species. Brauer (1906) figures *G. vanhoeffeni* with lateral line organs on the caudal rays much as in *longicirra* but does not mention this unusual phenomenon in the text.

Although the standard length of the present specimen is only 40% of that of the largest specimen of *Gigantactis* yet taken (the type of *G. macronema* Regan, 1925), one half of the types of previously known gigantactinids are smaller. Thus it would appear that the characters used to distinguish *G. longicirra* are no more likely to be juvenile than are those for half the members of the genus. Furthermore, it would not seem likely that the structural characteristics listed above (at least the first two) had been derived by growth or simplification as a stage in the life history of some previously known form. However, in the absence of any direct evidence concerning the changes which take place in *Gigantactis* in the course of its ontogeny, it is rather difficult to make any predictions concerning such aberrant forms.¹

LINOPHRYNE ALGIBARBATA, spec. nov. (Figs. 3 and 4)

1 specimen; holotype, M. C. Z. No. 35,066.

Total length 40 mm., standard length 28 mm. Illicium suprarrostral, length from articulation with basal bone to distal end of bulb 7 mm. (25% of S. L.), basal bone not exerted in present condition of specimen.² Bulb of esca 50% of length of illicial stem. Length of lower

¹ But see Fraser-Brunner's (1935) suggestion that the presence of teeth on the lower jaw well down on the sides of the chin and away from the bite of the jaws was a juvenile character in *Gigantactis*.

² Since the basal bone (modified pterygiophore) of the illicium is freely moveable and supplied among others with extensor and retractor muscles, the amount of its exertion in any specimen depends on the condition of these muscles on fixation. Clearly, however, certain forms such as *Mancalias* and *Lasiognathus* must always have a considerable portion of the basal bone exerted whereas others as *Edriolychnus* and *Himantolophus* do not.



Fig. 3. *Linophryne algibarbata*, spec. nov. Standard length 28mm.

jaw to articular spine 9 mm. (31% S. L.). Barbel length about 24 mm. (86% S. L.).

Sphenotic and preopercular spines large and sharp, free of skin except at their bases, smaller frontal and articular spines present.

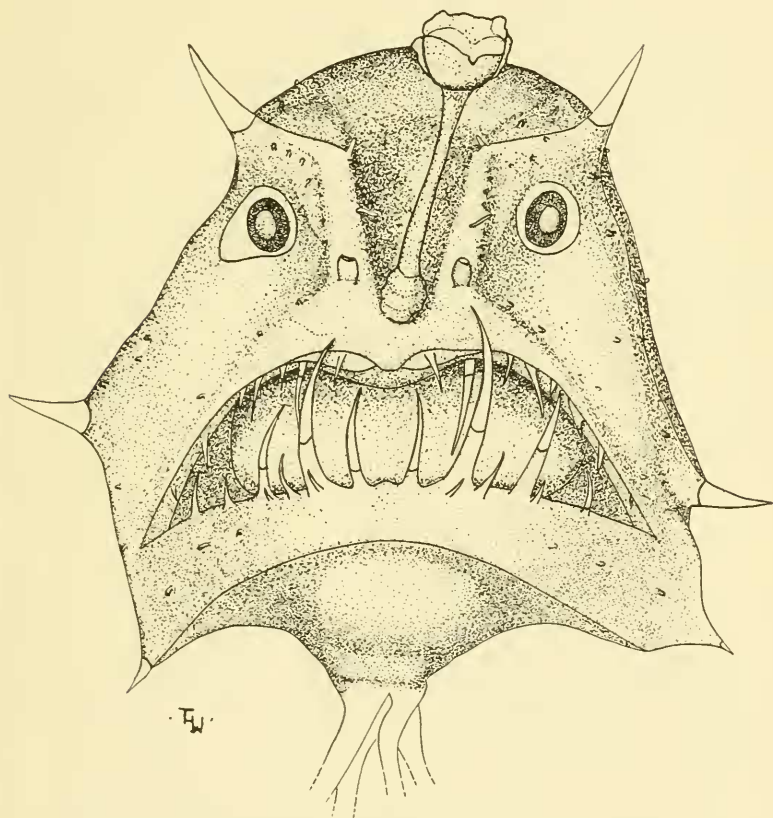


Fig. 4. *Linophryne algibarbata*, spec. nov.

Dentition. Teeth depressable inwards. Lower jaw: 7-8 irregularly arranged teeth including 1 very large (15% S. L.) and 2 smaller fangs on each side. Upper jaw: 7-8 irregularly arranged teeth including 1 large fang on each premaxillary; maxillary toothless. Large fangs saber-like, sheathed proximally in pigmented epithelium. Lower

pharyngeals toothless, 3 teeth each on second and third upper pharyngeals (pharyngobranchials). Palatines toothless; 2 teeth on vomer.

Fin rays. D.3, A.2, P.16. Brachiostegeal rays 4 (1+3); pectoral radials (pterygials) 3 (2+1). Pigmented skin runs out over all fin rays.

Barbel arises from short stalk which divides immediately into four main branches of approximately equal length and diameter; each of these gives rise to irregularly arranged, much shorter secondary and tertiary branches, which in most cases have knob-like swellings along their lengths and terminally.

Esca consists of a subspherical bulb bearing around its anterodorsal surface a roughly horse-shoe shaped ridge which consists of a median and two lateral lobes. In the median line, just posterior to this ridge is a low silvery papilla behind which is the external pore of the luminous organ of the esca. A slight longitudinal ridge of short extent is present immediately posterior to this. A black pigment cup which is visible through the transparent outer layers of the bulb surrounds about half of an inner sphere (the light organ), the exposed, distal part of which appears silvery. The rim of this pigmented cup has two distinct notches in it, one anterior, which is visible in Fig. 4, and one posterior.

The nostrils are large and tubular; lateral line organs are present on the head and body; these are situated on tags of pigmented skin, a few of which are notably larger than the rest. No channels or grooves connect these organs.

No pelvic bones were found in a dissection of one side of the specimen.

The skin is smooth and (after fixation in formalin followed by alcohol) chocolate brown in color.

Type locality. 39°06'N., 70°16'W., July 20th, 1937; closing net, 400 m., 5 A.M., depth to bottom 2860 m.

Discussion

In recent papers Regan and Trewavas (1932) and especially Parr (1934) have organized and extended our knowledge of the genus *Linophryne*. Twenty-five specimens belonging to this genus have been reported in the literature. For the twenty-one of these which are adequately known thirteen species and five subspecies have been defined. Thus nine species and two subspecies are known only from single specimens. In no case has more than one fish of a species in this genus been taken in a single catch.

The characteristics which distinguish *L. algibarbata* most clearly from any of these previously known species are as follows:

1. The absence of either terminal or lateral filaments or of digitiform appendages on the esca. These occur in all other known species in some form or combination.

2. The general pattern and the method of branching of the hyoid barbel. While this appendage is similar in a general way to that of *L. arborifera* and of *L. macrodon*, it differs distinctly from these not only in the fact that the four main branches are of approximately equal length and diameter but also in the details of the secondary and tertiary ramifications.

3. Presence of only 4 branchiostegal rays instead of the 5 which Regan and Trewavas (1932) had concluded from their dissections of *L. racemifera*, *Halpophryne* sp., and *Aceratias indicus* were characteristic of the Family *Linophrynidae*. However, the present observation shows that more specimens will have to be investigated before the significance of this point for diagnostic purposes will be apparent.

Since the present specimen differs from forms previously described in the fundamental pattern of the barbel and of the terminal appendages of the esca, it is clear that a new species is necessary here rather than a subspecies, such as those set up in *Linophryne arborifera* and *L. coronata* by Parr (1934) on the basis of minor variations in the details of these structures.

DOLOPICHTHYS ALBIFILOSA, spec. nov. (Figs. 5 and 6).

♂ specimen; holotype, M. C. Z. No. 35,067.

Total length 45 mm., standard length 33 mm. Illicium suprafrontal, length from articulation with basal bone to distal end of esca bulb 14 mm. (41% S. L. or 2.4 times as long as the exerted part of the basal bone in the present condition of the specimen¹). Bulb of esca about 20% of length of illicium from basal bone articulation. Length of lower jaw 14 mm. (41% S. L.); lower jaw with symphysial spine. Large sharp sphenotic spines present; also 2 articular spines on each side, less than half the size of the sphenotics.

Fin rays. D.5, A.5, P.17. Branchiostegal rays 6 (2+4); pectoral radials (pterygials) 3 (1+2).

Dentition. Teeth slender and acicular, depressable inwards. Lower jaw: 24 teeth on each side arranged in three series of different sizes. Upper jaw: 24 in a single series on each premaxillary (only 7-8 of these evident without partial dissection); maxillary toothless. Up-

¹ See footnote 2, p. 85.

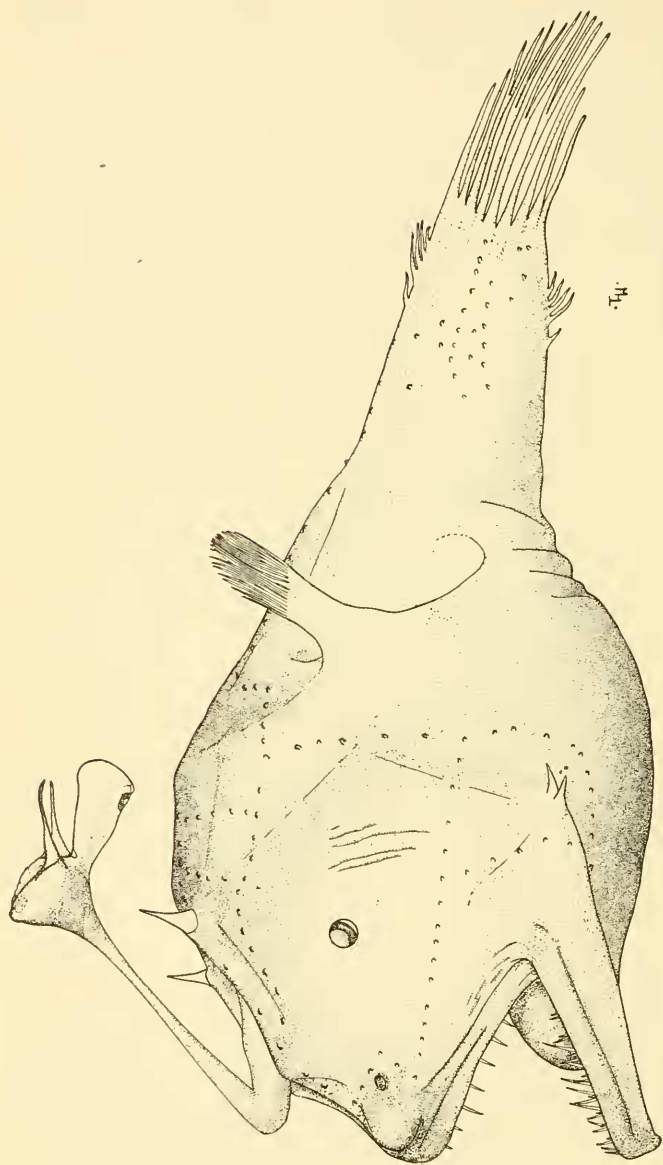


Fig. 5. *Dolopichthys albiflosa*, spec. nov. Standard length 33 mm.

per and lower pharyngeals and palatines toothless. Two teeth on each side of vomer.

The esca¹ (Fig. 6) consists of a laterally compressed terminal expansion of the illicium enclosing within it an ovoid bulb. On the median anterior aspect of the latter is a low papilla projecting anterodorsally. Just posterior to this and running laterally are two slightly raised areas; between these and in the median line is a ridge which runs posteriorly and bifurcates over the posterior portion of the bulb. Each limb of this bifurcation gives rise to a stout, rapidly tapering filament one-fourth as long as the illicium from basal bone articulation to distal end of bulb. A loose transparent layer of tissue covers the distal part

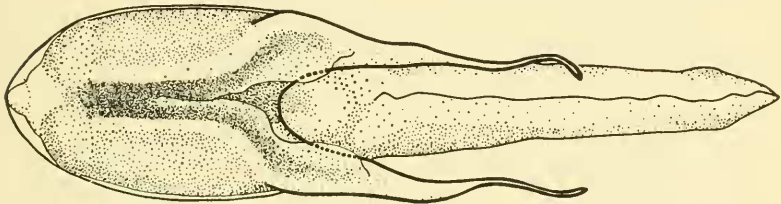


Fig. 6. Dorsal view of esca of *Dolopichthys albiflosa*, spec. nov.

of the bulb and terminates posteriorly in a little upstanding ruffle on the antero-median surface of each of the esca filaments. Posterior to the latter and in the median sagittal plane the esca bulb bears a large vane-like, laterally compressed appendage three-tenths as long as the illicium. Distally on the ventral margin of this appendage there is a subspherical heavily pigmented body with a ventrally directed white spot (light organ?). The remaining pigmentation of the whole structure is as follows: the inner bulb of the esca, the proximal part of the latter where it expands from the illicial stem, and the median ridge running posteriorly from the papilla, are all heavily pigmented. The two raised areas just behind and lateral to the papilla, the ventral part of the compressed appendage and the anteromedian aspect of the esca filaments are lightly pigmented by a few scattered granules. The remaining parts of the esca including the rest of the two filaments are whitish.

The nostrils are short and tubular with two openings distally; lateral

¹ The present description of the esca is made with the orientation of this organ in the living animal in mind. "Posterior" and "anterior" are reversed in relation to Regan and Trewavas' (1932) use of these terms.

line organs on tags or flaps of pigmented skin with terminal white spots are present on the head and body. An unusual aggregation of these organs occurs caudally between the opposed soft dorsal and anal fins.

A pelvic bone was found in a dissection of one side of the specimen. The skin is smooth and jet black.

Type locality. "Atlantis" Station 2667 (35°40'N., 69°36'W.), depth of haul unknown, September 1936.

Discussion

It is clear that the present specimen is closely related to *Dolopichthys nigrifilis* Regan and Trewavas (1932, p. 67). There are, however, a number of distinct differences between them:

1. The esca filaments of *D. albiflosa* are almost entirely free of pigment, whereas the proximal four-fifths of the same appendages in *nigrifilis* are heavily pigmented.¹

2. These same filaments in the new species are only one-fourth of the length of the illicium from basal bone-articulation to distal end of the bulb; in *nigrifilis* they are about one-half this length or relatively twice as long.

3. In *albiflosa* the stalk of the illicium is heavily pigmented and this pigment runs out distally so far that it covers one-half of the terminal expansion containing the illicial bulb. In *nigrifilis* neither the illicial stalk nor its terminal expansion are so pigmented (Regan and Trewavas, 1932, Fig. 92).

4. The compressed esca appendage in *albiflosa* is somewhat longer relative to the length of the illicium and it is rather more lightly pigmented than it is in *nigrifilis*.

5. The illicium is only 40% rather than 50% of the standard length in the new species.

6. In the present specimen the illicium distal to the basal bone-articulation is only 2.5 times the length of the exerted part of the pterygiophore whereas in *nigrifilis* it is six times this length (see, however, footnote 2, p. 85).

7. The cleft of the mouth in *albiflosa* does not extend posteriorly to the level of the eye whereas it extends behind the eye in Regan and Trewavas' (1932) specimen of *nigrifilis*.

¹ It is worth pointing out that the type specimen of *D. albiflosa* was so little damaged when it arrived on deck that it lived for a short time in chilled sea water (see preceding section, p. 71); presumably then such an absence of pigment as mentioned above may well be considered natural rather than due to damage in capturing the specimen.

8. The dentition of the two species would appear to be significantly different; *albifilosa* has 60% more teeth in the upper jaws, and 30% more in the lower than *nigrifilis*. This fact is difficult to evaluate since we do not as yet have any data on the individual or ontogenetic differences in the teeth of ceratioids.¹

9. The only known specimen of *nigrifilis* is from the China Sea (19°18.5'N., 120°13'E.) whereas *albifilosa* is from the western Atlantic.

The above differences which distinguish the new species from its nearest relative are thus seen to be rather small, and when considered separately some of them are of questionable importance. Nevertheless, they are of the same order of magnitude as those which have been used to establish a great many of the species of this genus (compare, for example, *D. pilotus*, *D. multifilis*, and *D. claviger* Regan and Trewavas, 1932, p. 73). From the ninety-three specimens of *Dolopichthys* which have been taken forty-six species have been described; twenty-nine (63%) of them are monotypic. The distinctions between the various members of the genus are, however, of two principal orders of magnitude so that Regan and Trewavas (1932) have distinguished between these by grouping certain of the species differing inter se by such characters as minor variations in the esca pattern into five subgenera which are characterized by differences of a more fundamental nature.² In spite of the small amount of material available for comparative study and in spite of the slight variations which have been used in establishing many species, from their wide experience Regan and Trewavas (1932, p. 71) feel that most of the species will prove in the future to be valid.

In view of these facts the establishment of a new species for the present specimen would seem to be quite in keeping with the precedent for the genus.

¹ See Fraser-Brunner, 1935, for discussion of evidence for possible ontogenetic changes in the dentition of *Gigantactis*.

² Parr (1934, p. 41ff.) in his revision of the genus *Linophryne* has accomplished the same sort of distinction between the relative importance of characters by the alternative method of setting up sub-species.

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